ZooKeys 20: 127–153 (2009)
doi: 10.3897/zookeys.20.119
www.pensoftonline.net/zookeys

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Masner, a new genus of Ceraphronidae (Hymenoptera, Ceraphronoidea) described using controlled vocabularies

Istvan Mikó†, Andrew R. Deans‡

I *Insect Museum, Department of Entomology, North Carolina State University, Campus Box: 7613, Raleigh, NC. 27695-7613, USA*

† *urn:lsid:zoobank.org:author:07136805-7B7A-490B-BB08-86556F7A6129*
‡ *urn:lsid:zoobank.org:author:7FE1A5BC-A6C3-4055-98EC-9B54A3A5A786*

Corresponding authors: *Istvan Mikó* (istvan.miko@gmail.com), *Andrew R. Deans* (andy_deans@ncsu.edu)

Academic editor: *Norman Johnson* | Received 04 March 2009 | Accepted 03 June 2009 | Published 14 September 2009

urn:lsid:zoobank.org:pub:8F4C743C-DAD0-4D89-AE53-46E1711E91CE

Citation: Mikó I, Deans AR (2009) *Masner*, a new genus of Ceraphronidae (Hymenoptera, Ceraphronoidea) described using controlled vocabularies. In: Johnson N (Ed) Advances in the systematics of Hymenoptera. Festschrift in honour of Lubomír Masner. ZooKeys 20: 127–153. doi:10.3897/zookeys.20.119

Abstract

A ceraphronid wasp genus, *Masner* Mikó & Deans, **gen. n.**, with one species, *M. lubomirus* Deans & Mikó, **sp. n.** is described from Australia and Fiji based on male specimens. This new genus challenges previous definitions of the two extant ceraphronoid families by sharing some character states with Megaspilidae (the presence of an expanded pterostigma and an occipital depression) and other character states with Ceraphronidae (the presence of uniramous anterior protibial spur, presence of a comb of the spur on the pro- and mesotibial spurs, a single mesotibial spur, an undivided synsternite, the presence of axillular setae, presence of Waterston's evaporatorium and the fusion of the parossiculus with the gonostipes). *Masner* is distinguishable from all other Ceraphronoidea by the sensillar patch present on flagellomere 5 but absent from flagellomeres 6–9 and the presence of a dorsally visible depression surrounding anterior part of the petiole. The limits of Ceraphronidae and Megaspilidae are reviewed, and we provide new characters for family level diagnosis and classification. We also hypothesize that *Masner* is sister to the remaining Ceraphronidae.

Keywords

morphology, terminology, anatomy, Hymenoptera, ontology

Copyright *I. Mikó & A.R. Deans*. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Ceraphronoidea is a demonstrably monophyletic lineage (Dowton and Austin 2001, Hymenoptera Tree of Life project in prep., Ronquist et al. 1999), comprised of two moderately sized extant families[1] – Ceraphronidae, with 301 valid species in 14 genera, and Megaspilidae, with 299 valid species in 13 genera (Johnson and Musetti 2009) – and recognized by the fused C+R extending along the anterior margin of the fore wing, the ventrally articulated antennae, the curved fore wing r-rs crossvein, and the presence of two tibial spurs on the fore leg (Dessart and Cancemi 1987; Masner 1993; Westwood 1832).

Their biology is difficult to define, and most references describe ceraphronoid wasps as parasitoids of late-instar insects in weak concealment (e.g., Gauld and Bolton 1988). Several species are known to negatively impact biological control systems (Boenish et al. 1997; Evans et al. 2005; Höller et al. 1993; Oatman 1985; Sullivan et al. 1999), especially *Aphanogmus* (Ceraphronidae). *Dendrocerus* spp. (Megaspilidae: Megaspilinae), which span the breadth of trophic levels from primary to quaternary parasitoid, have been used as model systems for understanding the ecology of parasitoidism (Chow and Mackauer 1999; Mackauer and Völkl 2005; Zuparko and Dahlsten 1995). Few other hymenopteran taxa exhibit the range of host diversity seen in Ceraphronoidea. The genus *Dendrocerus*, for example, has been reared from five orders of insect host (Fergusson 1980): Hemiptera, Neuroptera, Coleoptera, Diptera, Hymenoptera. Other ceraphronoids are known to parasitize Thysanoptera, Mecoptera, and Trichoptera (Luhman et al. 1999; Cooper and Dessart 1975; Dessart and Bournier 1971).

We currently have no published large-scale phylogeny of this lineage, but the extant families appear to be monophyletic (Deans and Murray in prep.) and are easily diagnosed using several discrete characters (Dessart 1995b, c; Dessart and Cancemi 1987; Masner and Dessart 1967; Masner 1993):

pterostigma: (0) large in Megaspilidae (except in fully winged Lagynodinae males), (1) reduced in Ceraphronidae.

female flagellomere number: (0) 9 in Megaspilidae, (1) 8 in Ceraphronidae.

mesotibial spur number: (0) two mesotibial spurs in Megaspilidae, (1) one mesotibial spur in Ceraphronidae.

fore leg calcar (0) bifid in Megaspilidae, (1) not bifid in Ceraphronidae.

Waterston's evaporatorium: (0) unmodified acrotergite of metasomal tergum 6 in Megaspilidae, (1) presence of evaporatorium in the acrotergite of metasomal tergum 6 that is associated with a putative exocrine gland in Ceraphronidae.

---

[1] The extinct family Stigmaphronidae (and sometimes even Maimetshidae) is also included within Ceraphronoidea (Carpenter 1992, Rasnitsyn 1991) based on the enlarged hind coxa, the relatively ventral articulation of the antennae on the lower face, and the curved fore wing r-rs. We do not treat Stigmaphronidae and Maimetshidae here.

anterior synsternite: (0) with anterior separated area in Megaspilidae, (1) with no separated area in Ceraphronidae.

Lubomír Masner played critical roles in ceraphronoid systematics by 1) placing these wasp families into their own superfamily independent of Proctotrupoidea (Masner 1956), and 2) morphologically delimiting the families and subfamilies, in part, by the character states described above (Masner and Dessart 1967), and 3) proposing the main hypothesis of higher-level ceraphronoid relationships (Masner and Dessart 1967, fig. 40). Through his industrious efforts to collect, sort, mount, label, and re-sort specimens, and by enthusiastically communicating important discoveries, Lubo continues to promote interest in ceraphronoid taxonomy. His encyclopedic knowledge, energy, and willingness to train the next generation of ceraphronoid experts sustain the hope that this fascinating lineage of insects will not wallow in neglect.

Lubo shared one of his discoveries with IM during a recent visit to Ottawa: two lots of specimens that blur the traditional boundaries between Ceraphronidae and Megaspilidae by having only one apical spur on mesotibia while bearing a distinct pterostigma on the fore wing. Lubo has a long history of bringing new taxa to light, instantiated by the descriptions of *Pteroceraphron* Dessart (Dessart 1981), *Retasus* Dessart (Dessart 1984), and *Aetholagynodes* Dessart (Dessart 1994b), as well as the revisions of *Cyoceraphron* Dessart (Dessart 1994a) and *Lagynodes* Förster (Dessart 1987b) and descriptions of many new species (e.g., Dessart 1994b) that are based on Masner-sorted CNCI material (see the acknowledgments of these papers). We continue this parade of discovery by describing new taxa and by briefly discussing the impacts of these observations on our understanding of Ceraphronoidea taxonomy.

Materials and methods

Specimens were borrowed from the South Australian Museum, Adelaide, South Australia (SAMA), and acquired from the collecting efforts of the Fiji Biodiversity of Arthropods (FBA). Specimens will be deposited in SAMA, the Fiji National Insect Collection, Suva (FNIC), the Canadian National Collection of Insects (CNCI) and the North Carolina State University Insect Museum (NCSU). Digital images were made using an Olympus CX41 compound microscope and DP71 digital camera. SEM micrographs were made using a Hitachi S-3200 Scanning Electron Microscope (wd=23.5, av=5kV). Specimens were critical point dried and coated with palladium prior to examination. For confocal laser scanning microscopy (CLSM) specimens were dissected, and parts of male genitalia were embedded in glycerin gelatin and in type VII agarose. Series of images were taken using a Leica inverted DM IRBE CLSM with a planachromat 40× 1.4 NA oil immersion objective. Videos generated through microscopy are available from the North Carolina State University Insect Museum website and from Google Video; links are in the appendix.

In an effort to use unambiguous terms in our taxon descriptions and to make semantic statements about the phenotypes of these taxa we employed several ontolo-

gies (i.e., controlled vocabularies) available from the Open Biomedical Ontologies Foundry (OBO Foundry[2]): Units of Measurement Ontology (UO[3]; date: 04:03:2009 17:16), Spatial Ontology (BSPO[4]; date: 08:12:2008 21:42), and the Phenotype and Trait Ontology (PATO[5]; date: 30:03:2009 16:12). Anatomical terminology follows the Hymenoptera Anatomy Ontology[6] (HAO; Deans et al. 2009) and includes terms from Ronquist and Nordlander 1989, Schulmeister 2001, Mikó et al 2007 and Vilhelmsen et al. 2009. New anatomical terms were added to the HAO and are provided below with *genus-differentia* definitions (Neuhaus et al. 2004; Smith 2005). We worked to manually compose our descriptions as collections of entity-quality (E-Q) statements, whereby the anatomical structure is the entity and the phenotype descriptor(s) represents the quality – e.g., mesodiscrimen (= entity) foveolate (= quality) (see Mabee et al. 2007a,b for discussion).

anterior mesopleural area (**ama**: Figs 1C, 6B): The area that is limited posteriorly by the anterior mesopleural sulcus.

anterior mesopleural sulcus (**ams**: Figs 1C, 6B): The sulcus that extends between the lateral end of the acetabular carina and the dorsal margin of the mesopleuron anterior to the mesopleural wing articulation. [Note: the anterior mesopleural sulcus is usually foveolate in Ceraphronoidea]. anterolateral mesoscutal corner (aem: Fig 1E): The corner that is located anterolaterally on the mesoscutum and is adjacent to the dorsal pronotal corner.

apical parossiculal seta (**asp**: Figs 3C, 4A, 6E; =soie subapicale Dessart and Gärdenfors 1985): The seta that is located submedially on the apical margin of the parossiculus.

axillular carina (**aux**: Figs 1C, F, 6B; Mikó et al 2007): The carina that delimits the axillula from the mesoscutellum (=scutellar carina Polaszek and Dessart 1996, =carénes latérales Dessart 1994b). [Note: The axillular carina is present usually only posteriorly on the mesoscutellum in Ceraphronoidea].

axillular setae (**axs**: Figs 1C, F, 6B): The row of setae that extends along the median margin of the axillula. [In Ceraphronoidea the row of axillular setae is parallel to the axillular carina (if latter is present)].

basal grooves: The row of grooves that extends along the anterior margin of an abdominal tergum or an abdominal sternum (=cannelure basale; Dessart and Gärdenfors 1985).

dorsal mesometapleural carina (**dmc**: Fig. 1C, 6B): The carina that extends along the dorsal margin of the mesometapleuron.

dorsal pronotal corner (**dpp**: Fig. 1E, 6B): The corner that is located submedially on the dorsal margin of the pronotum and that is adjacent to the anterolateral mesoscutal corner.

facial pit (**fp**: Fig. 6A; Bin and Dessart 1983; =fossette frontale Dessart 1966, =fosette scrobale Dessart and Gärdenfors 1985, =pore facial Dessart 1992): The pit that is located on the upper face dorsal to the intertorular carina and corresponds internally to a conical apodeme and not the tentorium.

facial sulcus (Dessart 1978): The sulcus that arises medially from the ventral margin of the median ocellus and extends towards the intertorular carina [Note: the facial sulcus is usually foveolate in Ceraphronoidea].

frontal scrobe (fdp: Fig. 6D; Mikó et al. 2007; =supraclypeal depression Dessart 1978, =dépression supraclypéale Dessart 2001): The scrobe that is located on the upper face. [Note: in Ceraphronoidea, the frontal depression extends ventrally between toruli.]

gonostipes (gsp: Figs 3C, 6E; Schulmeister 2001; =lamina parameralis Masner and Dessart 1967): The sclerite that is connected proximally with the cupula, distally with the harpe, ventrolaterally with the parossiculus.

harpe (**hrp**: Figs 3C, D, 4A, 6E; Schulmeister 2001)=paramères (Dessart and Gärdenfors 1985): The sclerite that is located distally of the gonostipes.

interaxillar sulcus (**ias**: Fig. 1D; =trait axillaire Dessart and Gärdenfors 1985): The sulcus that extends medially between the posterior margin of mesoscutum and the anterior margin of mesoscutellum.

interocellar pit (Bin and Dessart 1983; =pore interocellaire Dessart 1992): The pit that is located on the upper face between lateral ocelli and corresponds internally with a conical apodeme and not the tentorium.

interorbital space (=faciale interoculaire Dessart and Gärdenfors 1985): The anatomical line that marks the shortest distance between inner orbits.

intertorular carina (**itc**: Figs 1A, 6A, D; =carène intertorulaire, Dessart 1978): The carina that extends between the dorsal margin of toruli.

lateral propodeal carina (**lpc**: Fig. 1D, F, 6B; Mikó et al 2007; =carène propodéale transverse Dessart 2001): The carina that is oblique and arises from the median part of the anterior margin of the propodeum and extends to the posterior propodeal projection.

mesometapleural sulcus (**mts**: Fig. 1C): The sulcus that crosses the mesometapleuron from the posterolateral margin of the mesocoxal foramen to the mesopleural pit. [Note: The mesometapleural sulcus represents the border between the mesopleuron and metapleuron. The mesometapleural sulcus corresponds to a ridge and could be homologous with the mesepimeral ridge, which is definitely part of mesopleuron (Vilhelmsen et al. in press, Mikó et al 2007). In most Hymenoptera the mesopleuron extends past the mesepimeral ridge (not in Cynipoidea), and therefore its posterior margin is not easily delimited by the ridge, making uncertain the exact location of the border between meso- and metapleura based on the ridge and sulcus (=sillon mesopleuro-métopleurale; Dessart 1991, =mesometapleural suture, Vilhelmsen et al. in press).]

mesometapleuron: The sclerite that is comprised of the fused meso- and metapleura [Note: The border between meso- and metapleura is usually indistinct].

longitudinal metacoxal carina (**cxc**: Fig. 6B): The carina that is longitudinal and is located on the metacoxa [Note: In Ceraphronoidea the longitudinal metacoxal carina usually corresponds to rows of elongated setae and delimits a posterior concave area.]

metanotal-propodeal sulcus (**mps**: Fig. 1D, F, 6B; =foveole métanotale, Dessart 1994b, sillon métanotal Dessart 1996): The sulcus that extends along the anterior margin of the fused metanotum and propodeum and delimits an anterior narrow, usually differently sculptured area. [Note: The sulcus could mark the border between metanotum and propodeum or could be homologous with the metanotal trough (Mikó et al. 2007).]

ocellar fovea (**of**: Fig. 1A, 6D; =petite fossette triangulaire Dessart 2001): The depression that extends along the lateral margin of a lateral ocellus or along anterior margin of the imiko ocellus. [Note: If both preocellar pit and ocellar fovea are present, preocellar pit located within ocellar fovea (fig. X.1. Bin and Dessart 1983).]

occipital depression (**od**: Figs 1B): The depression that is located submedially on the occiput, ventral to the occipital carina.

parossiculus (**prs**: Fig. 3C, 6E; Schulmeister 2001; =plaques volsellaires Dessart and Gärdenfors 1985): The sclerite that is connected distally with the gonossiculus, laterally with the gonostipes and proximally with the gonostipital arm.

posterolateral pronotal area (**pla**: Fig. 1E; =prépectus; Dessart 1994b): The area that is delimited anteriorly by the posterolateral pronotal sulcus.

posterolateral pronotal carina (**ppc**: Fig. 1C): The carina that extends parallel to the posterolateral margin of the pronotum and delimits the posterolateral margin of pronotum. [Note: This structure might be homologous to the prepectus (Gibson 1999).]

posterolateral pronotal sulcus (**pps**: Figs 1C, E): The sulcus that arises from the ventrolateral pit of pronotum and reaches the posterolateral carina of the pronotum ventral to the anterior thoracic spiracle. [Note: Posterolateral pronotal sulcus and transverse pronotal sulcus compose a Y-shaped structure (=sillon en Y, sillon scapulaire Dessart 1996) in Ceraphronoidea.]

posterior mesoscutellar sulcus (pms: Fig. 1D) The sulcus that extends along the posterior margin of the mesoscutellum. [Note: The median part of the posterior mesoscutellar sulcus is usually foveolate between axillular carinae in Ceraphronoidea (=fovéoles apicales Dessart 1994b)].

postocellar furrow (=sillon postocellaire, Dessart 1995a): The sulcus that extends between the posterior margin of the lateral ocelli. [Note: In Ceraphronoidea this sulcus is usually foveolate].

preoccipital carina (**pc**: Fig. 6C; =carene préoccipitale; Dessart 1991): The carina that is transverse and extends posteriorly of the lateral ocelli and compound eye and delimits anteriorly the preoccipital lunula. [Note: The preoccipital carina might be homologous to hyperoccipital carina of Platygastroidea (Mikó et al. 2007).]

preoccipital furrow (**pof**: Figs 1A, 6C, D; Dessart 1978; =sillon préoccipital, Dessart 2001): The sulcus that arises medially from anterior margin of the occipital carina and extends towards the anterior ocellus.

preoccipital lunula (**pou**: Fig. 6C; Dessart 1978; =lunule préoccipitale Dessart 2001): The area that is concave, is located on the vertex and is limited anteriorly by the preoccipital carina and posteriorly by the occipital carina.

preocellar pit (**pp**: Fig. 6A; Bin and Dessart 1983; =pore preocellaire Dessart 1992): The pit that is located on the upper face adjacent the anterior margin of the median ocellus and corresponds internally to a conical apodeme and not the tentorium.

scutoscutellar sulcus (**sss**: Fig. 1D; Mikó et al. 2007; =sillon axillo-scutellaire Dessart 1994b). The sulcus that sets off the mesoscutellum from the mesonotum.

sensillar patch of the male flagellomere (**sp**: Figs 5B-E): The sensillar patch is located on the ventral surface of the male flagellomeres. [Note: The sensilla on the patch

differ from any other sensilla located on the male flagellomeres. The sensillar patch is absent from *Megaspilus*. In all *Ceraphron*, *Conostigmus* and *Dendrocerus* species without branched flagellomeres the sensillar patch is present on flagellomeres 5–9. In *Dendrocerus* species with branched flagellomeres the patch is present on flagellomeres 6–9. In *Masner* the patch is present only on flagellomere 5. In most Ceraphronoidea, where the patch is present, it bears basiconic sensilla and what might be release and spread structures (RSS: Isidoro et al 1996, M. Yoder pers. comm.). In *Aphanogmus*, the ventral sensillar patch has trichoid sensilla (M. Yoder pers. comm.).]

sensillum trichodeum curvatum (**stc**: Fig. 5E; Cave and Gaylor 1987): The seta that is curved. [Note: Sensillum trichodeum curvatum is present on the flagellomeres in all male *Ceraphron* and absent from all other Ceraphronoidea males including *Aphanogmus*].

syntergal translucent patch (**stp**: Fig. 2E): The translucent patch that is located submedially on the syntergum. [Note: The surface of the translucent patch is slightly differs from the surrounding surface.]

synsternal translucent patch (**stp**: Figs 2F, 7A, B): The translucent patch that is located on the synsternum.

synsternal setiferous patch (**smp**: Figs 2F, 7A, B): The setiferous patch that is on the synsternite. [Note: The setiferous patch might be homologous with the felt field of Platygastroidea (Mikó et al. 2007).]

transscutal fissure (**tsa**: Fig. 1D; Mikó et al 2007; =sillon mésoscutal transverse Dessart 1994b): The fissure that separates the mesoscutum from the rest of the mesonotum.

transverse carina of petiole (**tlt**, **tls**: Figs 2E, F; Vilhelmsen et al. in press; =col gastral Dessart and Gärdenfors 1985, =basal metasomal carina Polaszek and Dessart 1996): The carina that delimits the anterior vertical area of the petiole (synsternum+syntergum).

transverse pronotal sulcus (**tps**: Figs 1C, E; Vilhelmsen et al. in press): The sulcus that corresponds to the anteromedian pronotal ridge.

ventral pronotal pit (vpp: Figs 1C, 6B): The evaporatorium that is located medially on the acrotergite of metasomal tergum 6. [Note: The ventral pronotal pit corresponds to the medially projected ventral part of the pronotum and is usually covered with dense setae in Ceraphronidae.]

vertex/mouthparts transverse section: The transverse section that bisects the head from dorsal to ventral (in prognathous and opisthognathous hymenopterans) or anterior to posterior (in hypognathous hymenopterans).

Waterston's evaporatorium (wo: Figs 4C-F, =Waterston's organ Ogloblin 1944; =L'organe de Waterston Dessart 1992): The area that is located medially on the acrotergite (Packer 2004) of T6 and is modified for releasing glandular products. [Note: The Waterston's evaporatorium is a median, concave, calyx-like structure (wo: Fig. 4D, F) surrounded posteriorly by strongly sculptured cuticle in most Ceraphronidae, whereas it is a strongly sculptured area without any concave anterior part in Masner (wo: Fig. 4C, E). Waterston (1923) originally hypothesized, that this cuticle modification has a respiratory function. Later both Ogloblin (1944) and Dessart (1992) assumed that the structure corresponds to an opening of exocrine glands and could have evolved as an

increased evaporative surface. Different forms of cuticle modifications are known in Hymenoptera around the opening of type III exocrine glands (Noirot and Quennedey 1974, Buckingham and Sharkey 1988, Quicke 1990). We have located glands (g: Fig. 4F) connected to the lateral part of the calyx-like via ducts (d: Fig. 4F) in *Aphanogmus* and *Ceraphron*. Ogloblin proposed the term Waterston's organ for the cuticle modification on metasomal tergum 6 described by Waterston (1923): "tergite iv with anteromedianly the remarkable reticulated chitinous ring." Although Ogloblin (1944) suggested that Waterston's structure might have glandular function, he never described any corresponding glands and applied the term "Waterston's organ" exclusively to the cuticle modification. According to the Common Anatomy Reference Ontology (Haendel et al. 2007) a simple organ is a multi-tissue structure. Because this cuticular modification is not a multi-tissue structure we prefer to replace "organ" with "evaporatorium" from the heteropterists' lexicon. Evaporatorium refers to a modified cuticular structure associated with the opening of an exocrine gland, the purpose of which is to enlarge the evaporative surface (Carayon 1962; Torre-Bueno 1989).

Masner Mikó & Deans, gen. n.

urn:lsid:zoobank.org:act:FC311FF2-E57A-4CB1-B524-A07228D60911
Figs 1A-4C, 4E, 5A-B; see also Morphbank[7][collection 470970]

Type species: *Masner lubomirus* Deans & Mikó, sp. n. by monotypy and current designation.

Diagnosis. *Masner* gen. n. is distinguishable from all other Ceraphronoidea by three character states: the sensillar patch present on flagellomere 5 but absent from flagellomeres 6–9 (sf: Figs 5A, B), dorsally visible depression surrounding anterior part of the petiole and the irregular areolate sculpture of the dorsal cranium. It differs from all other Ceraphronidae in presence of pterostigma (sg: Fig 3A) and occipital depression (od: Fig. 1B). *Masner* gen. n. belongs to Ceraphronidae on the basis of the presence of calcar comb, absence of anterior mesotibial spur, uniramous anterior protibial spur (calcar), absence of anteriorly delimited narrow region of synsternite, presence of axillular setae and parossiculus fused with gonostipes and presence of Waterston's evaporatorium.

Etymology. The new genus group name is the Latinized family name of Lubomír Masner, who discovered the unique character combination of *Masner* gen. n., the presence of pterostigma on the wing and lacking posterior apical mesotibial spur and presorted the specimens of the new genus. Gender is masculine.

Masner lubomirus Deans & Mikó, sp. n.

urn:lsid:zoobank.org:act:0C66C345-7F28-4C6B-9FD1-131CDD07AA28
Figs 1A-4C, 4E, 5A-B

Description. *Body length*: 1.0–1.7mm (n=21, median=0.92)

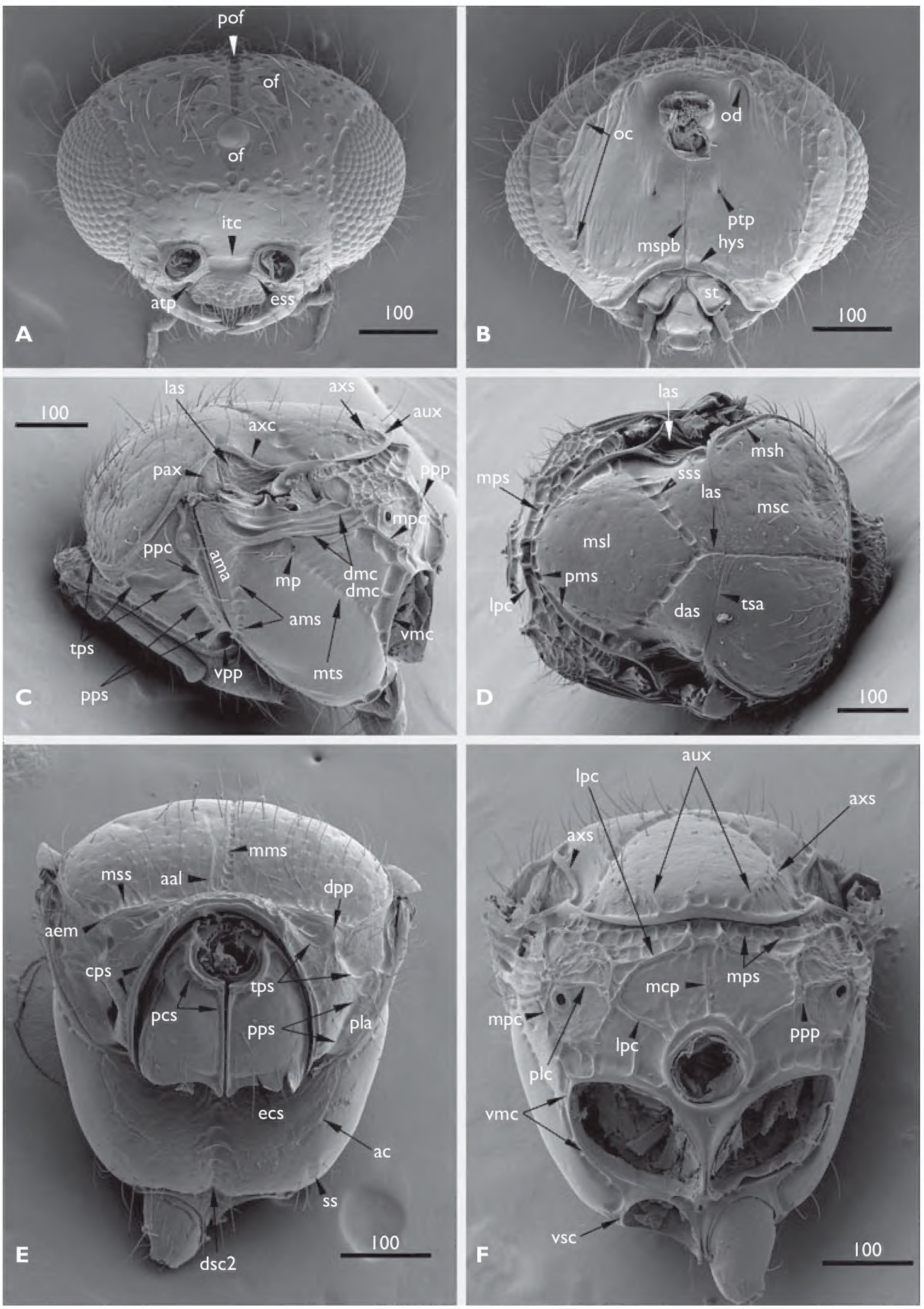

Figure 1. *Masner lubomirus* Deans and Mikó, sp. n. **A** head, anterior view **B** head posterior view **C** mesosoma lateral view **D** mesosoma dorsal view **E** mesosoma anterior view **F** mesosoma posterior view. Scale bars in micrometer.

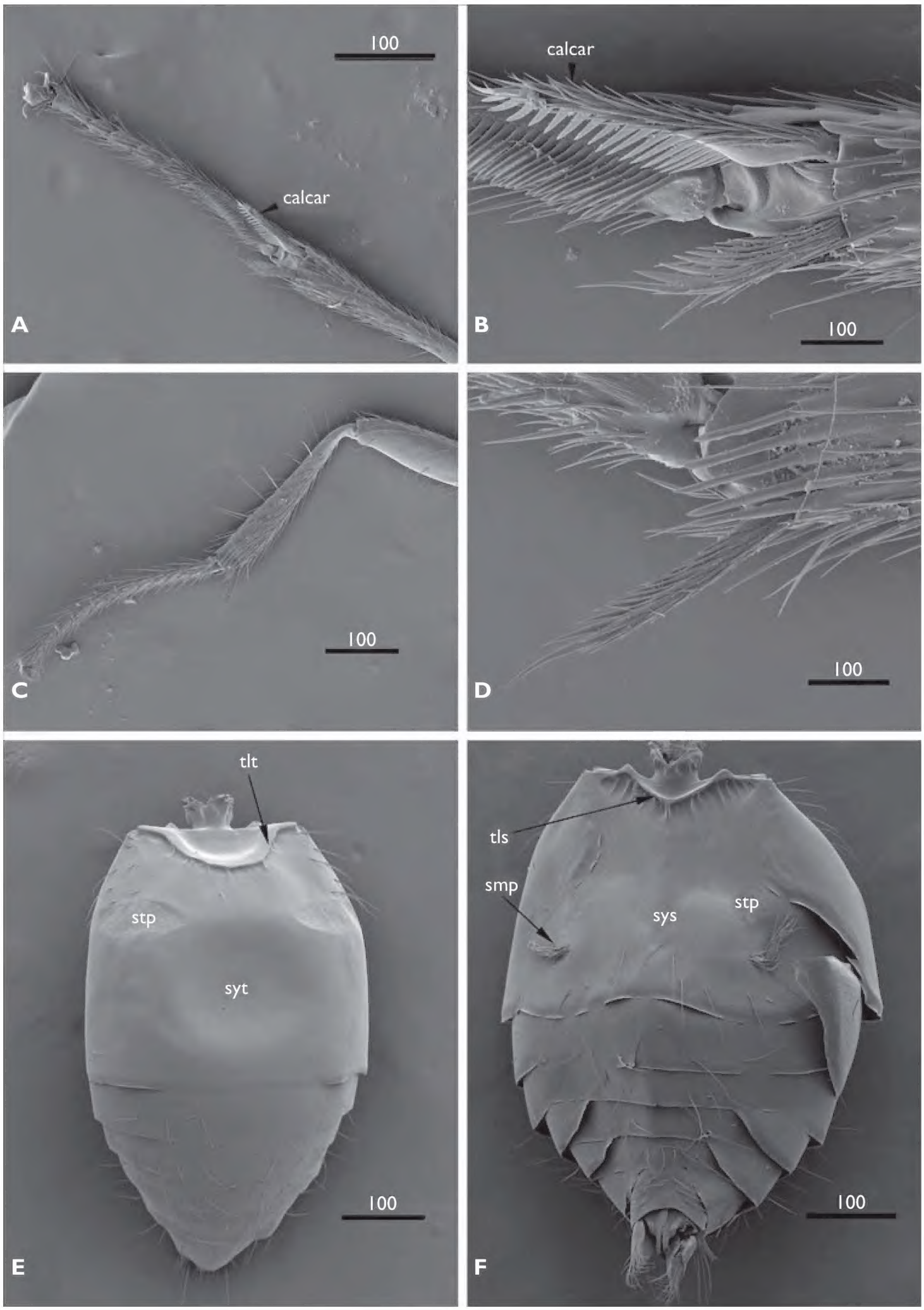

Figure 2. *Masner lubomirus* Deans and Mikó, sp. n. **A, B** protarsus and protibia, median view **C, D** mesotarsus and mesotibia, median view **E–F** metasomal, dorsal view, ventral view. Scale bars in micrometer.

Color: body brown, (with) low variability of color; maxillo-labial complex yellow; mandible yellow; blade brown; clypeus yellow; radicle yellow; scape yellow; pedicel yellow; leg yellow; tegula yellow; wing base yellow; syntergum yellow; synsternite yellow; male genitalia yellow.

Head: anterior side (part of cranium) elliptic, widest at medial region, height 1.4× length and width 1.25× height anterior side (part of compound eye) 2× as long as wide; setae (part of cranium) sparse, long, adpressed; setae (part of compound eyes) sparse, long, adpressed; setae (part of mandible) sparse, long, adpressed; setae (part of maxillo-labial complex) sparse, long, adpressed; epistomal sulcus distinct laterally, indistinct medially (**ess**: Fig. 1A), extending between structured anterior tentorial pits (**atp**: Fig. 1A); anterior side (part of clypeus) trapezoidal, slightly raised medially; ventral margin (part of clypeus) slightly concave, wider than long, granulose; punctures (part of clypeus) scattered, associated with setae; setae (part of clypeus) recumbent, longer than clypeus height; malar area granulose; area between torulus and epistomal sulcus granulose; margin (part of torulus) raised; lateral margin (part of torulus) increased height (relative to remaining margin); intertorular carina unstructured (**itc**: Figs 1A, 6D); crenulae (part of upper face) present in vicinty of torulus, slightly reticulate; foveae (part of upper face) dorsal to torulus, irregular; frontal scrobe absent; vertex reticulate; gena reticulate; foveae (part of vertex) irregular; foveae (part of gena) irregular; OOL:POL:LOL=2.3:1:1; ocellar foveae distinct (**of**: Figs 1A, 6D); ocellar foveae width equal to ocellus diameter; preocellar pit absent; facial pit absent; facial sulcus absent; preoccipital furrow structured, crenulate, in contact with anterior ocellus (**pof**: Fig. 1A, 6E); preoccipital carina absent; preoccipital lunula absent; occipital carina crenulate (**oc**: Fig. 1B); occipital depression present (**od**: Fig. 1B); occiput smooth; postgena smooth; crenulae (part of occiput) curved externally, in contact with occipital carina; posterior tentorial pit distinct, closer to occipital foramen than to oral foramen (**ptp**: Fig. 1B); postgenal suture present (**mspb**: Fig. 1B); hypostomal sulcus present, unsculptured (**hys**: Fig. 1B); stipes rectangular (**st**: Fig. 1B); medial margin (part of stipes) notched; anterior margin (part of stipes) notched; maxillary palp divided into 4 palpal segments; labial palp whole; mandible cleft; dorsal tooth shorter than ventral tooth.

Antenna: scape 2.5× as long as pedicel; flagellomere 2 2.5× as long as pedicel; flagellomere 3 2.5× as long as pedicel; flagellomere 4 2.5× as long as pedicel; flagellomere 5 2.5× as long as pedicel; flagellomere 6 2.5× as long as pedicel; flagellomere 7 2.5× as long as pedicel; flagellomere 8 2.5× as long as pedicel; flagellomere 1 2.75× as long as pedicel; flagellomere 9 3× as long as pedicel; flagellum as wide as pedicel, cylindrical, covered with adpressed setae, pedicel as long as wide (Fig. 5A); scape wider than pedicel; scape cylindrical, covered with adpressed setae, lenght about 2× width (Fig. 5A); 3 rows of sensilla (part of sensillar patch part of flagellomere 5) present (**sp**: Fig. 5B); sensillum trichodeum curvatum (part of flagellum) absent (e.g. **stc**: Fig. 5E).

Mesosoma: pronotal cervical sulcus crenulate (**cps**: Fig. 1E), in contact with ventral pronotal pit (**vpp**: Fig. 1C); ventral pronotal pit distinct, bare; median pronotal area

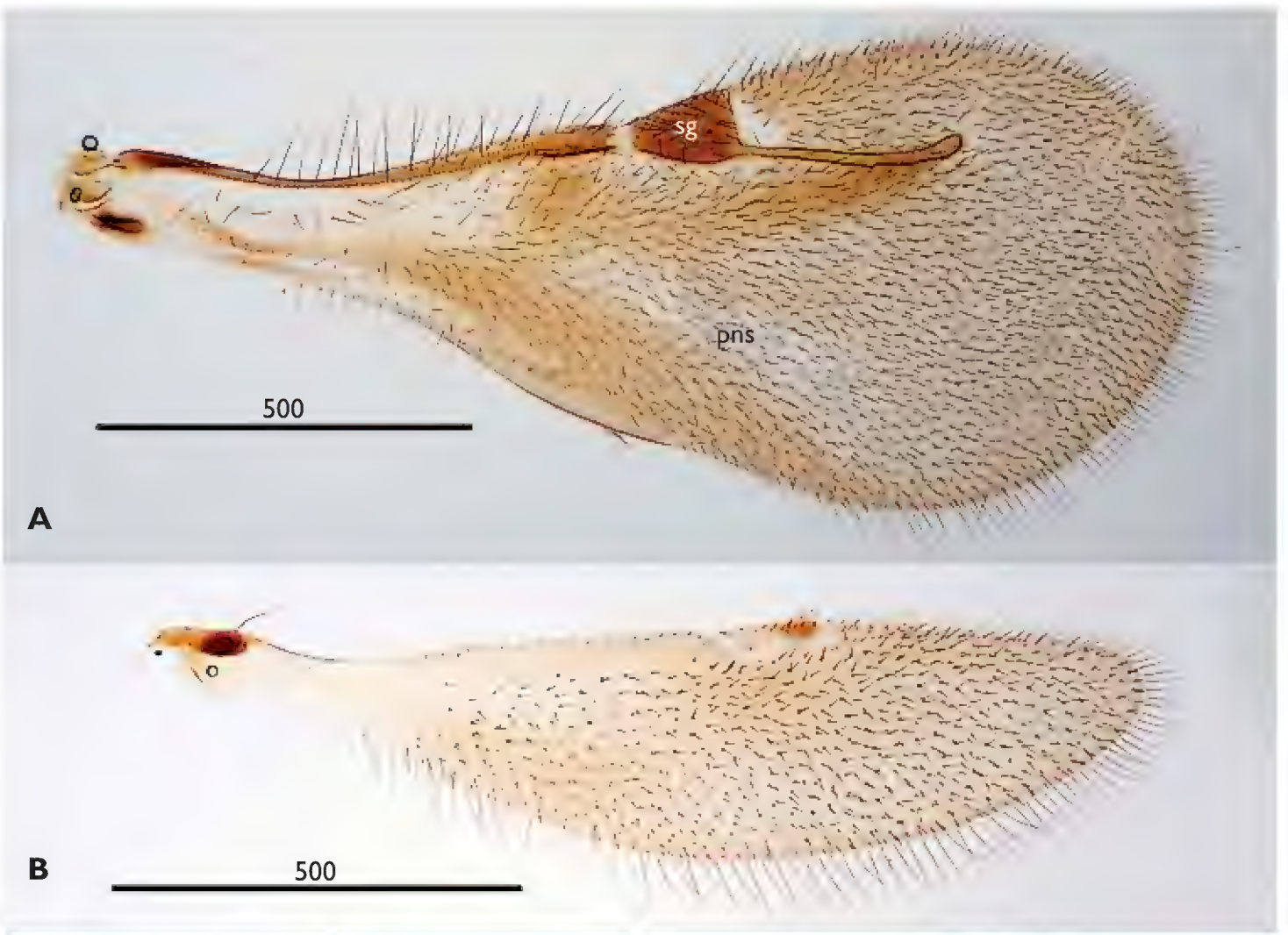

Figure 3. *Masner lubomirus* Deans and Mikó, sp. n. **A** Fore wing **B** hind wing **C** male genitalia, ventral view **D** male genitalia, dorsal view. Scale bars in micrometer.

raised, granulose; dorsal pronotal region corner indistinct (**dpp**: Fig. 1E); transverse pronotal sulcus crenulate medially (**tps**: Figs 1C, E), in contact with posterolateral pronotal sulcus (**pps**: Figs 1C, E) above midlevel; posterolateral pronotal sulcus shallow; posterolateral pronotal area narrow (**pla**: Fig. 1E), reticulate; propleuron smooth; epicoxal sulcus (**ecs**: Fig. 1E) present medially; propleural cervical sulcus present ventrally along medial margin of propleuron (**pcs**: Fig. 1E); mesoscutum finely reticulate, sparsely setose; setae (part of mesoscutum) elongate, curved posterior; mesoscutellum finely reticulate, sparsely setose; setae (part of mesoscutellum) elongate, curved posterior; dorsal axillar area finely reticulate, sparsely setose; setae (part of dorsal axillar area) elongate, curved posterior (**msc**, **msl**, **das**: Fig. 1D); mesoscutum 2× as wide as long; median mesoscutal sulcus (**mms**: Fig. 1E) crenulate anteriorly, continuous posteriorly; interaxillar sulcus present (**ias**: Fig. 1D); anteroadmedian line indistinct; distance from anteroadmedian line to median mesoscutal sulcus equal to anterior sulcus width (**aal**: Fig. 1E); mesoscutal suprahumeral sulcus crenulate medially, unsculptured laterally of anterolateral mesoscutal region corner (**mss, aem**: Fig. 1E); mesoscutal humeral sulcus distinct, unsculptured (**msh**: Fig. 1D); notaulus absent; parapsidal line absent; posterior margin (part of mesoscutum) concave; preaxilla smooth (**pax**: Fig. 1C); lateral axillar area reticulate; 3–4 carinae (part of lateral axillar area) present posteriorly (**las**: Figs 1C, D); scutoscutellar sulcus angled medially, foveolate; fovea (part of scutoscutellar sulcus) 2× as wide as long (**sss**: Fig. 1D), continuous with interaxillar sulcus (**ias**: Fig. 1D); mesoscutellum length equal to width; axillular carina present posteriorly, absent anteriorly (**aux**: Figs 1C, F); posterior mesoscutellar sulcus (**pms**: Fig. 1D) crenulate between axillular carinae, extending anteriorly along lateral margin of axillula and in contact with axillar carina (**axc**: Figs 1C, F); anterior mesopleural sulcus crenulate; anterior mesopleural area finely reticulate (**ams**, **ama**: Fig. 1C); posteroventral area (part of mesopleuron) smooth; acetabular carina tapered medially (**ac**: Fig. 1E); acetabulum reticulate; depression (part of subpleural signum) shallow (**ss**: Fig. 1E); sternaulus absent; mesodiscrimen foveolate (**dsc2**: Fig. 1E); 3–4 dorsal mesometapleural carinae present (**dmc**: Fig. 1 C); dorsal mesometapleural carinae straight; anterior mesopleural sulcus perpendicularly intersecting mesometapleural carinae; mesometapleural sulcus present, crenulate, in contact with mesopleural pit (**mts**, **mp**: Fig. 1 C); mesopleural pit adjacent to ventralmost dorsal mesometapleural carina; ventralmost dorsal mesometapleural carina continuous with metapleural carina (**mpc**: Figs 1C, F); ventral metapleural carina (**vmc**: Figs 1C, F) contiguous with ventral mesopleural carina (**vsc**: Fig. 1F); ventral metapleural carina and ventral mesopleural carina foveolate; foveae (part of ventral mesopleural carina) rectangular, transverse, >2× as long as wide; foveae (part of ventral metapleural carina) rectangular, transverse, >2× as long as wide; metanotal-propodeal sulcus foveolate; 2 rows of foveae (part of metanotal-propodeal sulcus) present medially (**mps**: Figs 1D, F); lateral propodeal carina curved dorsolaterally, raised medially; 2 projections (part of propodeal carina) small (**lpc**: Fig. 1D, F); metasomal depression smooth; one median carina (part of metasomal depression) whole (**mcp**: Fig. 1F); one lateral carina (part of metasomal depression) whole, extending between small posterior propodeal

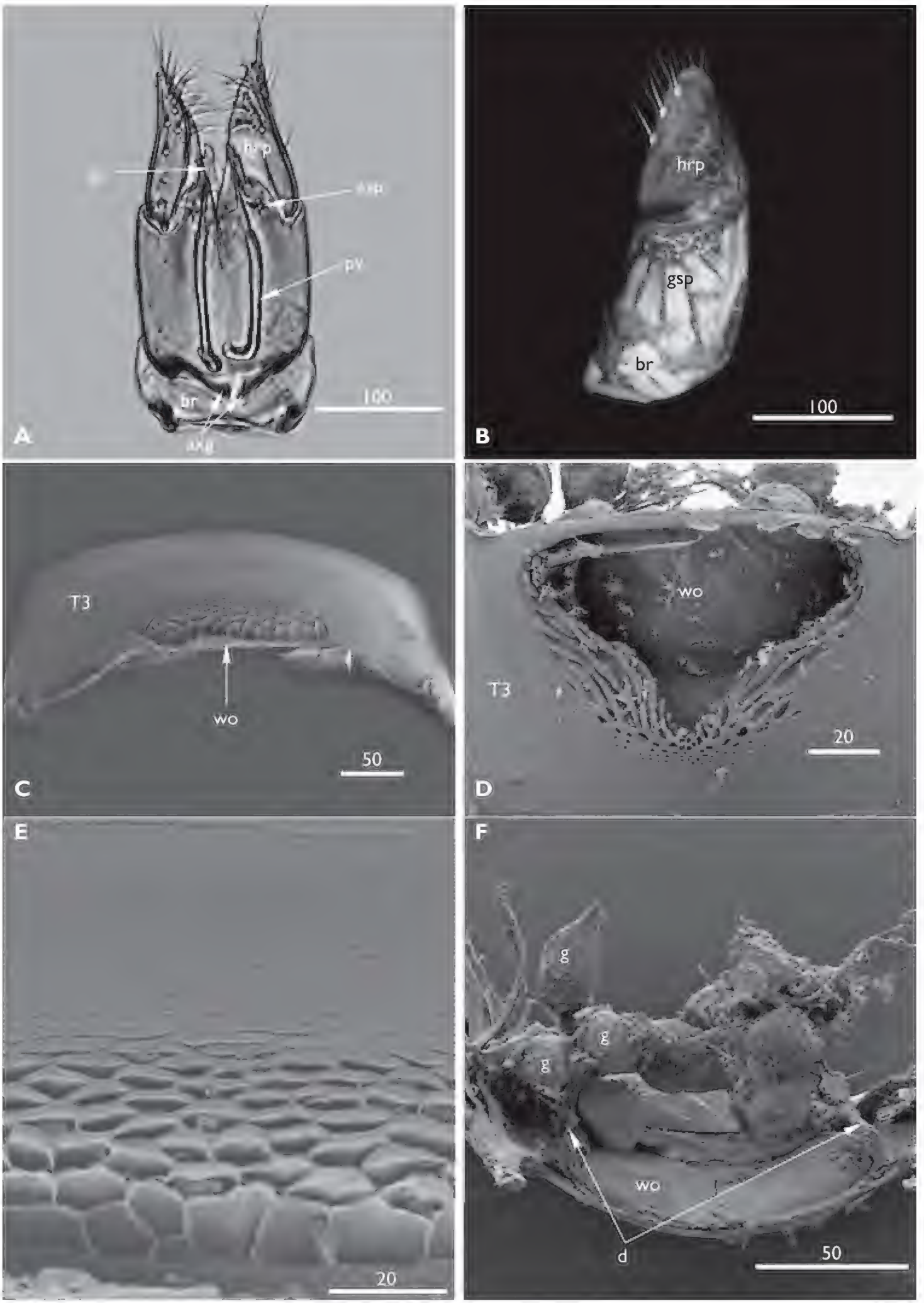

Figure 4. Male genitalia and Waterston's evaporatorium of Ceraphronidae **A–B** *Masner lubomirus* Deans and Mikó, sp. n., male genitalia **A** ventral view[8] **B** lateral view[9] **C–F** Waterston's evaporatorium **C** *Masner lubomirus* Deans and Mikó, sp. n., dorsal view **D** *Aphanogmus* sp. dorsal view **E** *Masner lubomirus* Deans and Mikó, sp. n. **F** *Aphanogmus* sp., anterior view. Scale bars in micrometer.

projections (**ppp**: Fig. 1C, F) and lateral part of propodeal foramen (**lcp**: Fig. 1F); plica present (**plc**: Fig. 1F).

Wings: Fore wing darkly pigmented, translucent, less melanized proximally; hind wing darkly pigmented, translucent, less melanized proximally; medial area (part of fore wing) unpigmented medially (**pns**: Fig. 3A; between pterostigma and posterior margin of fore wing); pterostigma 2× as long as wide; posterior margin (part of pterostigma) straight; lateral margin (part of pterostigma) slightly convex; r-rs crossvein straight, 4× as long as pterostigma width.

Legs: apical tarsomere plus pretarsus as long as tarsomeres 2–4; basitarsus as long as tarsomeres 2–5 (Figs 2A, C); longitudinal metacoxal carina absent.

Metasoma: syntergum smooth, wider than long; syntergal translucent patch transverse (**stp**: Fig. 2E); transverse carina (part of syntergum) present; basal grooves absent (**lmt**: Fig. 2E); metasomal tergum 3 reticulate (Figs 2E, 2F); metasomal tergum 4 reticulate; metasomal tergum 5 reticulate; metasomal tergum 6 reticulate; metasomal tergum 7; metasomal tergum 8 reticulate; transverse carina (part of synsternum) present; metasomal sterna smooth (Fig. 2F); anteromedian areolate area (part of Waterston's evaporatorium) surrounded posterolaterally by concentric sulci (Waterston's evaporatorium without calyx-like anterior area).

Male genitalia (see additional files: Movie1[8] and Movie2[9]) cupula prominent ventromedially (**cu**: Fig. 3C-4A); gonostipital arm oblique, oriented anteromedially (**axg**: Fig. 4A); harpe concave externally, conical, setose medially; setae (part of harpe) as long as proximal harpe width (**hrp**: Fig. 3C-4A); gonostipes as wide as long, fused dorsally; apical margin (part of gonostipes) cleft medially (**mig**: Fig. 3D); parapenis fused with gonostipes (i.e., not separated from gonostipes by apical incision) (**prp**: Fig. 3D); one seta (part of parossiculus) present apically (**asp**: Fig. 3C, 4A); penisvalva curved proximally (**pv**: Fig. 4A).

Etymology. The dense setae on the clypeus of *Masner lubomirus* resembles the recumbent pilosity on the chin of Lubomír Masner. Therefore the new specific epithet is the Latinized first name of Lubomír Masner, in the nominative singular case.

Material examined. Holotype male: **AUSTRALIA**: Queensland, Mount Glorious, 27°19'54"S 152°45'29"E, 7–13.II.1998, N.Power, T.Hiller, Malaise trap. Paratypes males: **AUSTRALIA**: Queensland, Mount Glorious, 27°19'54"S 152°45'29"E, 24–30.XI.1997, N.Power, T.Hiller, Malaise trap, 3 males; 24–30.I.1998, 4 males; 7–13.II.1998, 6 males; 24–30.X.1998, 1 male. **FIJI**: Vanua Levu, Macuata Prov. 0.4 km S Rokosalase Village, [-16.532°, 179.019°] 118m, 23.IV-8.V.2004 Malaise. Schlinger Tokota'a. FJVN57c_M02_03.FBA067015, 2 males, Taveuni, Cakaudrove Prov. 5.3 km SE Tavuki Village, Mt Devo1064m17–24.X.2002. Malaise 3. Schlinger, M. Tokota'a, 16.841° S, 179.968° W. FBA 098106. Holotype in SAMA, paratypes in CNCI, NCSU and FNIC.

Discussion. Ceraphronoidea is divided into two families: Ceraphronidae and Megaspilidae based on ten two-state characters that are, with one exception, invariable within each family (Table 2.). The pterostigma is present only in Megaspilinae, but absent in Lagynodinae and Ceraphronidae. This observation, and the considera-

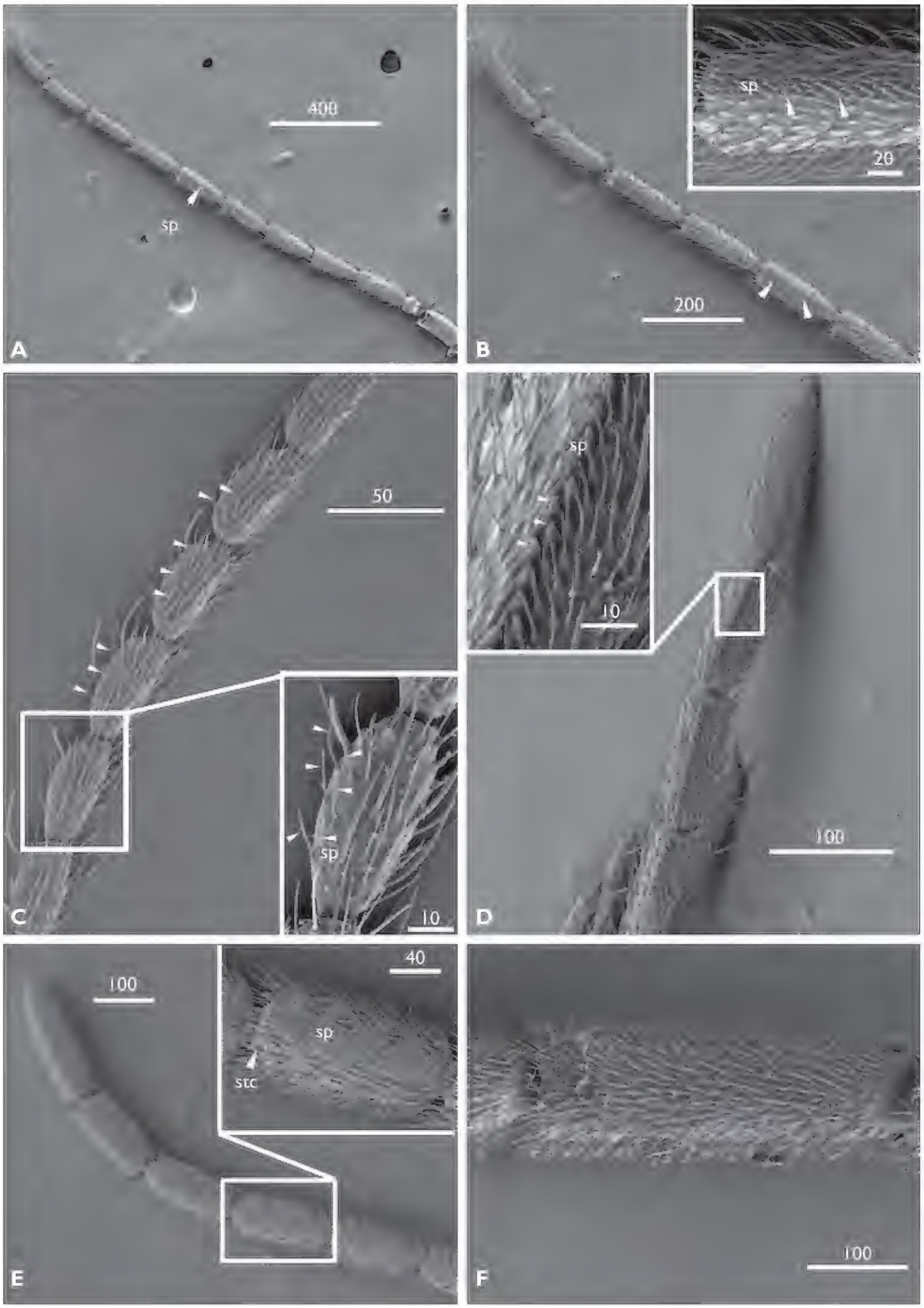

Figure 5. Male antenna of Ceraphronoidea **A–B** *Masner lubomirus* Deans and Mikó, sp. n. **C** *Aphanogmus* sp. **D** *Ceraphron* sp. **E** *Dendrocerus* sp. **F** *Megaspilus* sp. Unlabelled arrows indicate antennal sensilla located on sensillar patch. Scale bars in micrometer.

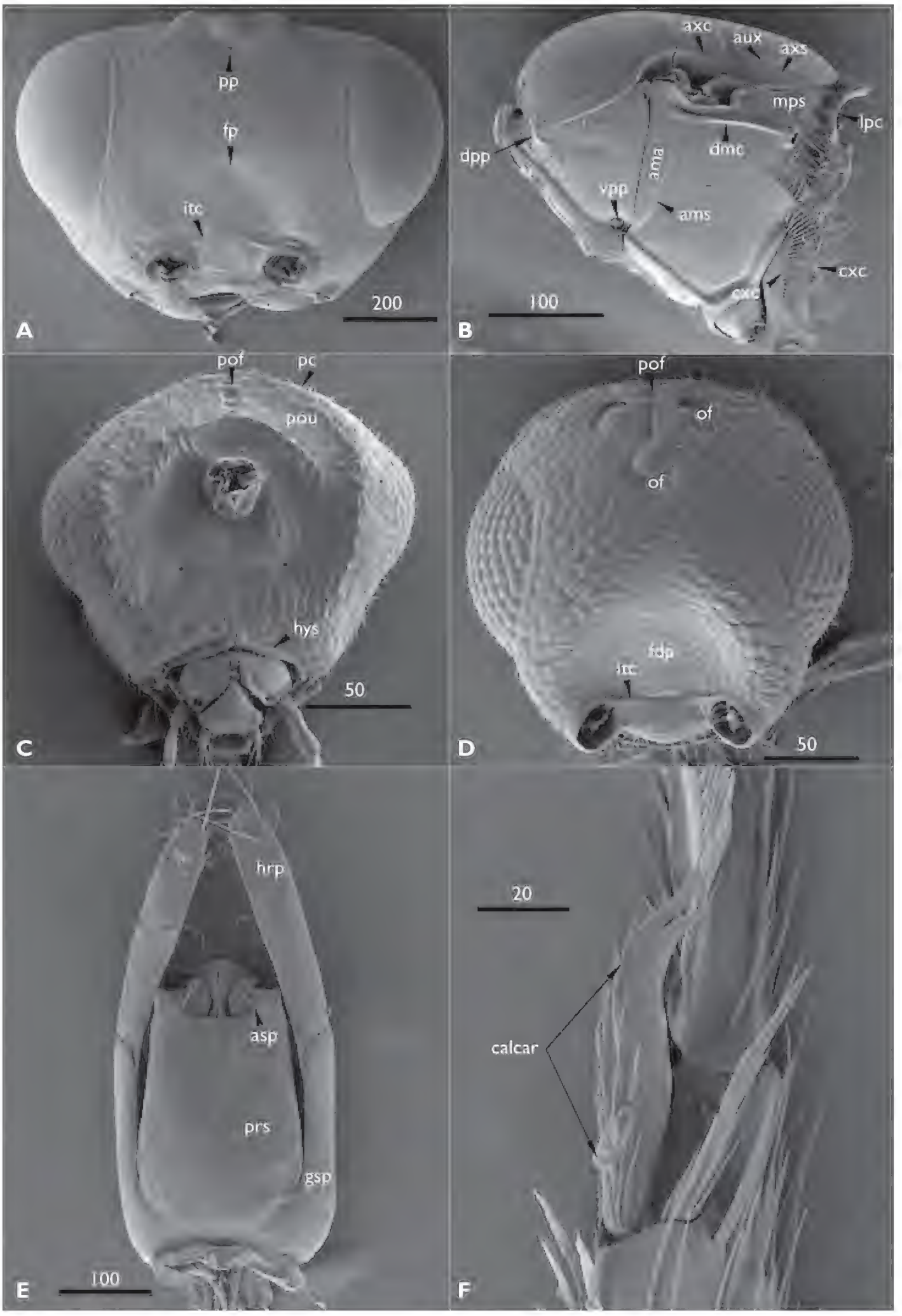

Figure 6. Ceraphronoidea **A** *Trichosteresis glabra*, head, anterior view **B** *Aphanogmus* sp., mesosoma, lateral view, anterior to the left **C** *Aphanogmus* sp., head, posterior view **D** *Aphanogmus* sp., head, anterior view **E** *Megaspilus* sp., male genitalia, ventral view **F** *Conostigmus* sp., apex of mesotibia, ventral view. Scale bars in micrometer.

tion of Bethylidae as the sister group of Ceraphronoidea led Masner and Dessart (1967) to assume that the absence of the pterostigma is the ground plan for the superfamily. Although the subfamily and generic classification of the superfamily is currently considered to be unstable, it is widely accepted that Megaspilidae and Ceraphronidae are two distinct and probably monophyletic taxa. Although the presence of non-overlapping two-state characters strongly support the latter hypothesis, it has

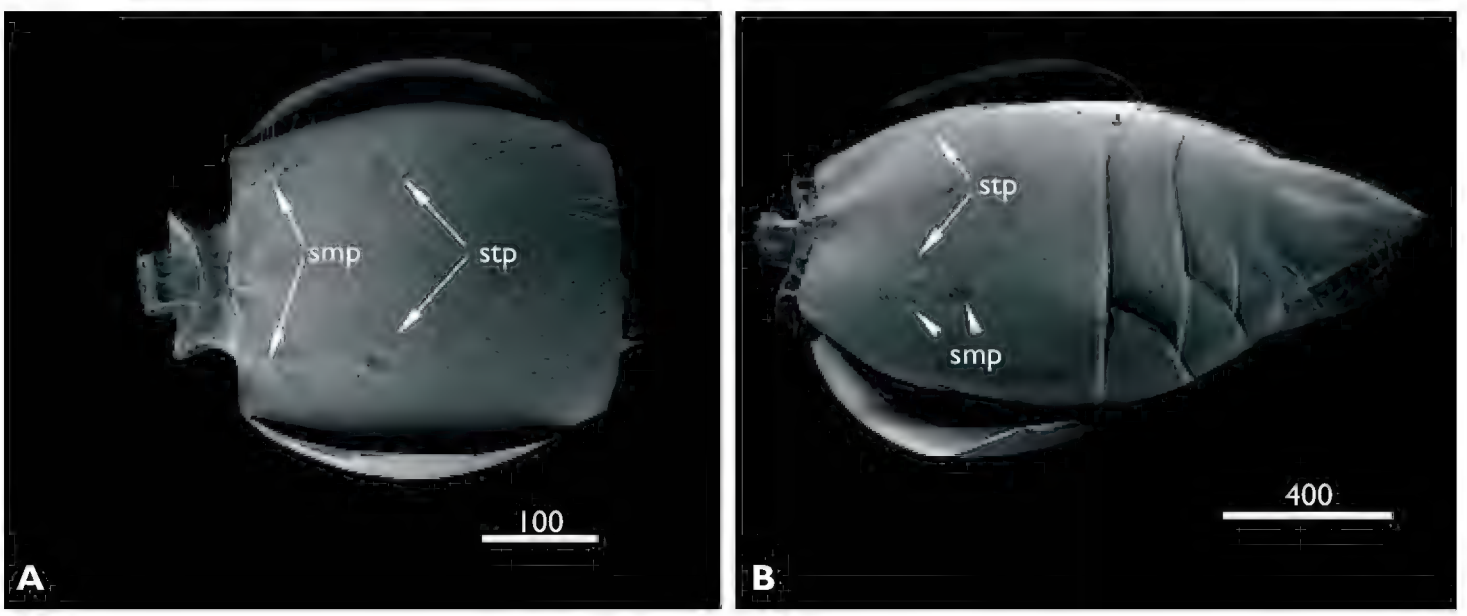

Figure 7. Ceraphronoidea **A–B** Metasoma, ventral view **A** *Trichosteresis glabra* **B** *Lagynodes* sp. **C** *Masner lubomirus* Deans and Mikó, sp. n., lateral view. Scale bars in micrometer.

Table 2. Characters for limiting Ceraphronoidea families (MD=Masner and Dessart 1967, BQ=Basibuyuk and Quicke 1995, oo=own observations).

character	**Ceraphronidae**	**Megaspilidae**	***Masner* gen. n.**
surface sculpture of calcar (BQ)	comb on the ventral face of calcar present (Figs 2A-D)	comb on the ventral face of calcar absent (Fig. 6F)	Ceraphronidae
apex of calcar (MD)	simple (**calcar**: Figs 2A, B)	bifid (**calcar**: Fig. 6F)	Ceraphronidae
number of mesotibial spur (md)	1 (Figs 2C, D)	2	Ceraphronidae
Waterston's evaporatorium (MD)	present (Figs 4C-F)	absent	Ceraphronidae
pterostigma (MD)	absent	present/absent	Megaspilidae
anterior part of synsternite (MD)	simple (Fig. 2F)	narrow sclerite separated (Figs 7A, B)	Ceraphronidae
parossiculus vs. gonostipes (MD)	fused (Fig. 3C, 4A)	separated (Fig. 6E)	Ceraphronidae
number of female flagellomeres (MD)	8	9 (except fossil *Lygocerus dubitatus* Brues 1937)	??
occipital depression (oo)	absent (Fig. 6C)	present (Figs 1B)	Megaspilidae
axillar setae (oo)	present (Fig. 1C, F)	absent	Ceraphronidae

never been tested phylogenetically. Overlapping characters in *Masner* weakens both of the above-mentioned hypotheses (apomorphic pterostigma and the dichotomous Ceraphronoidea). The presence of the Waterston's evaporatorium is an important character state that indicates *Masner* belongs in Ceraphronidae. The absence of the anterior calyx-like concave area and the presence only of sculptured cuticle, however, could be considered an ancestral state of Waterston's evaporatorium. The structure of Waterston's evaporatorium and the fact that *Masner* shares two family level characters with Megaspilidae leads us to hypothesize that this taxon is the sister to the remaining Ceraphronidae. Future work will focus on testing this hypothesis using molecular and morphological data.

Acknowledgments

We gratefully acknowledge the assistance of Chuck Mooney (North Carolina State University Analytical Instrumentation Facility) with scanning electron microscopy and Eva Johannes (NCSU-NSCORT Department of Botany, N.C. State University) with confocal laser scanning microscopy. We thank Matt Yoder for his valuable comments on antennal sensillum types, Bob Blinn for comments on the evaporatorium

and Lubomír Masner for his valuable comments regarding this new taxon. ARD gratefully acknowledges Wasila Dahdul, Jim Balhoff, Todd Vision, and the National Evolutionary Synthesis Center (NSF EF-0423641) for fostering his growing interest in the application of biomedical ontologies to biodiversity discovery. This research was enabled by a CANACOL Foundation grant to IM and by the National Science Foundation (DBI-0850223).

References

Austin AD (1983) Morphology and mechanics of the ovipositor of *Ceratobaeus* Ashmead (Hymenoptera: Scelionidae) and related genera. International Journal of Insect Morphology and Embryology 12: 139–155.

Austin AD, Field SA (1997) The ovipositor system of scelionid and platygastrid wasps (Hymenoptera: Platygastroidea): comparative morphology and phylogenetic implications. Invertebrate Taxonomy 11: 1–87.

Basibuyuk HH, Quicke DLJ (1995) Morphology of the antenna cleaner in the Hymenoptera with particular reference to non-aculeate families (Insecta). Zoologica Scripta 24: 152–177.

Bin F, Dessart P (1983) Cephalic pits in Proctotrupoidea Scelionidae and Ceraphronoidea (Hymenoptera). Redia 66: 563–575.

Boenisch A, Petersen G, Wyss U (1997). Influence of the hyperparasitoid *Dendrocerus carpenteri* on the reproduction of the grain aphid *Sitobion avenae*. Ecological Entomology 22: 1–6.

Buckingham GR, Sharkey MJ (1988) Abdominal exocrine glands in Braconidae (Hymenoptera). In: Gupta V (Ed) Advances in Parasitic Hymenoptera Research. E.J. Brill, Leiden/ New York, 199–242.

Carayon J (1962) Observations sur l'appareil odorifique des Hétéroptères particulièrment celui des Tingidae, Vianaididae et Piesmatidae. Cahiers des Naturalistes 18(1): 1–16.

Carpenter FM (1992) Arthropoda 4. Superclass Hexopoda. Treatise on Invertebrate Paleontology, Part R. The Geological Society of America, Boulder, CO. 655 pp

Cave RD, Gaylor MJ (1987) Antennal sensilla of male and female *Telenomus reynoldsi* (Hymenoptera: Scelionidae). International Journal of Insect Morphology and Embryology 16: 27–39.

Chow A, Mackauer M (1999) Host handling and specificity of the hyperparasitoid wasp, *Dendrocerus carpenteri*: importance of host age and species. Journal of Applied Entomology 123: 83–91.

Cooper KW, Dessart P (1975) Adult, larva and biology of *Conostigmus quadratogenalis* Dessart & Cooper, sp.n., (Hym., Ceraphronoidea), parasite of *Boreus* (Mecoptera) in California. Bulletin et Annales de la Societe Royale Belge d'Entomologie 111: 37–53.

Deans AR, Yoder MJ, Seltmann KC. Hymenoptera Glossary: http://purl.oclc.org/NET/hymontology. [Thu Feb 26 15:50:30 -0600 2009]

Dessart P (1966) Contribution a létude des Hyménoptères Proctotrupoidea. (XI) Revision des Ceraphronidae d'Afrique orientale decrits par l'Abbé Jean-Jacques Kieffer. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 42(19): 1–30.

Dessart P (1978) Four new species of African Ceraphronidae (Hymenoptera). Journal of the Entomological Society of South Africa 41: 275–284.

Dessart P 1981. Genres, espèces et sexe nouveaux d'Hyménoptères Ceraphronoidea. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 53(7): 1–21.

Dessart P 1984. *Retasus ater* gen. n., sp. n.: un ceraphronide de cauchemar! (Hymenoptera ceraphronoidea). Bulletin et Annales de la Société Royale Belge d'Entomologie 120: 277–281.

Dessart P (1987) Revision des Lagynodinae (Hymenoptera Ceraphronoidea Megaspilidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 57: 5–30.

Dessart P (1991) Considerations sur le genre *Synarsis* Foerster, 1878 (Hym. Ceraphronoidea Ceraphronidae). Bulletin et Annales de la Société Royale Belge d'Entomologie 127: 385–400.

Dessart P (1992) L'organe Waterston des Ceraphronidea (Hymenoptera Ceraphronoidea). Bulletin et Annales de la Société Royale Belge d'Entomologie 128: 203–212.

Dessart P (1994a) A propos du genre *Cyoceraphron* Dessart, 1975 (Hymenoptera Ceraphronoidea Ceraphronidae). Bulletin et Annales de la Société Royale Belge d'Entomologie 130: 19–52.

Dessart P (1994b) Hymenoptera Ceraphronoidea nouveaux ou peu connus. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Entomologie 64: 49–103.

Dessart P (1995a) Quelques considérations morphologiques pour l'étude des Hyménoptères Ceraphronoidea. Bulletin et Annales de la Société Royale Belge d'Entomologie 131: 319–326.

Dessart P (1995b) 8.5 Ceraphronidae. Pages 199–203 in Hanson, P and ID Gauld. Hymenoptera of Costa Rica. Oxford University Press, Oxford. 893 pp.

Dessart P (1995c) 8.6 Megaspilidae. Pages 203–208 in Hanson, P. and I. D. Gauld. Hymenoptera of Costa Rica. Oxford University Press, Oxford. 893 pp.

Dessart P (1996) Hymenoptera Ceraphronoidea nouveaux ou peu connus (no 2). Bulletin et Annales de la Société Royale Belge d'Entomologie 132: 45–62.

Dessart P (2001) Les Megaspilinae ni européens, ni américains 2. Les *Dendrocerus* Ratzeburg, 1852, à mâles non flabellicornés (Hymenoptera Ceraphronoidea Megaspilidae). Belgian Journal of Entomology 3: 3–124.

Dessart P, Bournier A (1971) *Thrips tabaci* Lindman (Thysanoptera), hôte inattendu *d'Aphanogmus fumipennis* (Thomson) (Hym. Ceraphronidae). Bulletin et Annales de la Societe Royale Entomologique de Belgique 107: 116–118.

Dessart P, Cancemi P (1987) Tableau dichotomique des genres de Ceraphronoidea (Hymenoptera) avec commentaries et nouvelles espèces. Frustula Entomologica 7-8: 307–372.

Dessart P, Gärdenfors U (1985) *Dendrocerus paradoxus* n. sp. et *D. ulmicola* n. sp. (Hym. Ceraphronoidea Megaspilidae), deux nouveaux hyperparasites palearctiques de pucerons. Bulletin et Annales de la Société Royale Belge d'Entomologie 121: 197–211.

Dowton M, Austin AD (2001) Simultaneous analysis of 16S, 28S, COI and morphology in the Hymenoptera: Apocrita – evolutionary transitions among parasitic wasps. Biological Journal of the Linnean Society (Zoology) 74: 87–111.

Evans GA, Dessart P, Glenn H (2005) Two new species of *Aphanogmus* (Hymenoptera: Ceraphronidae) of economic importance reared from *Cybocephalus nipponis* (Coleoptera: Cybocephalidae). Zootaxa 1018: 47–54.

Fergusson NDM (1980) A revision of the British species of *Dendrocerus* Ratzeburg (Hymenoptera: Ceraphronoidea) with a review of their biology as aphid hyperparasites. Bulletin of the British Museum of Natural History (Entomol.) 41: 255–314.

Gibson GAP (1999) Sister-group relationships of the Platygastroidea and Chalcidoidea (Hymenoptera) – an alternative hypothesis to Rasnitsyn (1988). Zoologica Scripta 28(1–2): 125–138.

Gould I, Bolton B (1996) The Hymenoptera. Oxford University Press, Oxford, UK 332pp.

Haendel MA, Neuhaus F, Osumi-Sutherland D, Mabee PM, Mejino JLV Jr, Mungall CJ, Smith B (2007) CARO-The Common Anatomy Reference Ontology. In Burger A, Davidson D, Baldock R. (Eds.) Anatomy Ontologies for Bioinformatics. New York: Springer. 311–333

Isidoro N, Bin F, Colazza S, Vinson SB (1996) Morphology of antennal gustatory sensilla and glands in some parasitoids Hymenoptera with hypothesis on their role in sex and host recognition. Journal of Hymenoptera Research 28: 206–239.

Johnson NF, Musetti L (2009) Hymenoptera Online Database. http://purl.oclc.org/NET/hymenoptera/hol /accessed 2 March 2009/

Luhman JC, Holzenthal RW, Kjaerandsen, JK (1999) New host record of a ceraphronoid (Hymenoptera) in Trichoptera pupae. Journal of Hymenoptera Research, 8(1): 126.

Mabee PM, Ashburner M, Cronk Q, Gkoutos GV, Haendel M, Segerdell E, Mungall C, Westerfield M (2007a) Phenotype ontologies: the bridge between genomics and evolution. Trends in Ecology & Evolution 22(7): 345–350.

Mabee PM, Arratia G, Coburn M, Haendel MA, Hilton EJ, Lundberg JG, Mayden RL, Rios N, Westerfield M (2007b) Connecting evolutionary morphology to genomics using ontologies: a case study from Cypriniformes including zebrafish. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, 308B: 655–668.

Mackauer M, Völkl W (2005) Sex ratio shift caused by hyperparasitism in the solitary parasitoid *Lysiphlebus hirticornis* (Hymenoptera: Braconidae: Aphidiinae). European Journal of Entomology 102: 475–481.

Masner L (1956) First preliminary report on the occurrence of genera of the group Proctotrupoidea (Hym.) in ČSR. (First part – family Scelionidae). Acta Faunistica Entomologica Musei Nationalis Pragae 1: 99–126.

Masner L, Dessart P (1967) La reclassification des categories taxonomiques superieures des Ceraphronoidea (Hymenoptera). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 43(22): 1–33.

Masner L (1993) Superfamily Ceraphronoidea. In: Goulet H, Huber JT (Eds) Hymenoptera of the World: An Identification Guide to Families. Research Branch, Agriculture Canada Publication 1894/E, Ottawa, 566–567.

Mikó I, Vilhelmsen L, Johnson NF, Masner L, Pénzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): head and mesosoma. Zootaxa 1571: 1–78.

Noirot C, Quennedey A (1974) Fine structure of insect epidermal glands. Annual Review of Entomology, 19: 60–80.

Neuhaus F, Grenon P, Smith B (2004) A formal theory of substances, qualities, and universals. A Varzi, L Vieu (eds.), Formal Ontology and Information Systems. Proceedings of the Third International Conference (FOIS 2004), Amsterdam: IOS Press, 2004, 49–58.

Oatman ER (1985) *Aphanogmus floridanus*, a primary parasite of *Feltiella acarivora*, a predator of spider mites on strawberry (Hymenoptera: Ceraphronidae; Diptera: Cecidomyiidae). Proceedings of the Entomological Society of Washington 87(4): 714–716.

Ogloblin AA (1944) Two new species of Proctotrupoidea from Iowa (Hymenoptera). Proceeding of the Entomological Society of Washington 46: 155–158.

Packer L (2004) Morphological variation in the gastral sterna of female Apoidea (Insecta: Hymenoptera). Canadian Journal of Zoology 82: 130–152,

Polaszek A, Dessart P (1996) Taxonomic problems in the *Aphanogmus hakonensis* species complex; (Hymenoptera: Ceraphronidae) common hyperparasitoids in biocontrol programmes against lepidopterous pestts in the tropics. Bulletin of Entomological Research 86: 419–422.

Quicke DLJ (1990) Tergal and intertergal metasomal glands of male braconine wasps (Insecta, Hymenoptera, Braconidae). Zoologica Scripta 19(4): 413 – 423.

Rasnitsyn AP (1991) Early Cretaceous members of evaniomorphous hymenopterans of the families Stigmaphronidae and Cretevaniidae and the subfamily Kotujellitinae (Gasteruptiidae). Paleontologicheskii Zhurnal 1991(4): 128–132.

Ronquist F, Nordlander G (1989) Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibaliidae). Entomologica Scandinavica Supplement 33: 1–60.

Ronquist F, Rasnitsyn AP, Roy A, Eriksson K, Lindren M (1999) Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data. Zoologica Scripta 28:13–50.

Schulmeister S (2001) Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, Symphyta). Acta Zoologica 82: 331–349.

Smith B (2005) The logic of biological classification and the foundations of biomedical ontology. in P Hájek, L Valdés-Villanueva, D Westerståhl (ed.), Logic, Methodology and Philosophy of Science. Proceedings of the 12th International Conference, King's College Publications, London 2005, 505–520.

Sullivan DJ, Völkl W (1999) Hyperparasitism: multitrophic ecology and behavior. Annual Review of Entomology 44: 291–315.

Vilhelmsen LB, Mikó I, Krogmann L (in press) Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in Apocritan wasps (Insecta: Hymenoptera). Zoological Journal of the Linnean Society.

Waterston J (1923) Notes on parasitic hymenoptera. Bulletin of Entomological Research 14: 103–118.

Westwood JO (1832) Description of several British forms amongst the parasitic hymenopterous insects. London & Edinburgh Philosophical Magazine and Journal of Science 1: 127–129.

Zuparko R, Dahlsten, DL (1995) Parasitoid complex of *Eucallipterus tiliae* (Homoptera: Drepanosiphidae) in Northern California. Environmental Entomology 24: 730–37.

Appendix I. Abbreviations used on figures

aal	anteroadmedian line
ac	acetabular carina
aem	anterolateral mesoscutal corner
ama	anterior mesopleural area
ams	anterior mesopleural sulcus
asp	apical parossiculal setae
atp	anterior tentorial pit
axc	axillar carina
aux	axillular carina
axg	apex gonostipitis
axs	axillular setae
cps	pronotal cervical sulcus
cu	cupula
cxc	longitudinal metacoxal carina
d	duct
das	dorsal axillar area
dmc	dorsal mesometapleural carinae
dpp	dorsal pronotal corner
dsc2	mesodiscrimen
ecs	epicoxal sulcus
ess	epistomal sulcus
fdp	frontal depression
fp	facial pit
g	gland-like structure
gsp	gonostipes
hrp	harpe
hys	hypostomal sulcus
ias	interaxillar sulcus
itc	intertorular carina
las	lateral axillar area
sys	synsternum
syt	syntergum
lcp	lateral carina of metasomal depression
lpc	lateral propodeal carina
mcp	median propodeal carina
mig	median incision of gonostipes
mms	median mesoscutal sulcus
mp	mesopleural pit
mpc	metapleural carina
mps	metanotal-propodeal sulcus
msc	mesoscutum
msh	mesoscutal humeral sulcus
msl	mesoscutellum
mspb	postgenal suture
mss	mesoscutal suprahumeral sulcus
mts	mesometapleural sulcus
oc	occipital carina
od	occipital depression
of	ocellar foveae
pax	preaxilla
pc	preoccipital carina
plc	plica
pns	pigmentless narrow strip on fore wing
ppp	posterior propodeal projection
pcs	propleural cervical sulcus
pla	posterolateral pronotal area
pms	posterior mesoscutellar sulcus
pof	preoccipital furrow
pou	preoccipital lunula
pp	preocellar pit
ppc	posterolateral pronotal carina
pps	posterolateral pronotal sulcus
prs	parossiculus
prp	parapenis
ptp	posterior tentorial pit
pv	penisvalva
shs	suprahumeral sulcus
smp	synsternal setiferous patch
sg	pterostigma
ss	subpleural signum
sss	scutoscutellar sulcus
st	stipes
stc	sensillum trichodeum curvatum
stp	synsternal and syntergal translucent patches

tls	transverse carina of petiole (on synsternite)
tlt	transverse carina of petiole (on syntergum)
tps	transverse pronotal sulcus
tsa	transcutal articulation

vmc	ventral metapleural carina
vsc	ventral mesopleural carina
vpp	ventral pronotal pit
sp	sensillar patch of male flagellomeres
wo	Waterston's evaporatorium

Appendix 2. URLs

http://www.zoobank.org/?id=urn:lsid:zoobank.org:pub:6B73E9F5-F4B7-442C-AE40-7D39D067E311 (manuscript LSID)
http://www.obofoundry.org/ (OBO Foundry)
http://www.obofoundry.org/cgi-bin/detail.cgi?id=unit (Units of Measurement Ontology)
http://www.obofoundry.org/cgi-bin/detail.cgi?id=spatial (Spatial Ontology)
http://www.obofoundry.org/cgi-bin/detail.cgi?id=quality (Phenotype and Trait Ontology)
http://purl.oclc.org/NET/hymontology (Hymenoptera Anatomy Ontology)
http://www.zoobank.org/?id=urn:lsid:zoobank.org:act:F0370F77-7CAB-4D9D-B583-50C514026357 (*Masner* Mikó & Deans ZooBank LSID)
http://morphbank.net/?id=470970 (Morphbank image collection for *Masner*)
http://www.zoobank.org/?id=urn:lsid:zoobank.org:act:A1C686F5-B6A7-44FC-A51C-7942DCF8371A (*Masner lubomirus* Deans & Mikó ZooBank LSID)
http://insectmuseum.org/MikoDeans2009a/Fig4B.avi (movie for Fig. 4B)
http://insectmuseum.org/MikoDeans2009a/Fig4A.wmv (movie for Fig. 4A) http://video.google.com/videoplay?docid=-7672031102854392911 (movie for Fig. 4A)
http://video.google.com/videoplay?docid=7261793710918450789 (movie for Fig. 4B)

Endnotes

[2] http://www.obofoundry.org
[3] http://www.obofoundry.org/cgi-bin/detail.cgi?id=unit
[4] http://www.obofoundry.org/cgi-bin/detail.cgi?id=spatial
[5] http://www.obofoundry.org/cgi-bin/detail.cgi?id=quality
[6] http://hymglossary.tamu.edu/projects/32/public/ontology/index
[7] http://www.morphbank.net/Show/?id=470970
[8] http://insectmuseum.org/MikoDeans2009a/Fig4A.wmv
[9] http://insectmuseum.org/MikoDeans2009a/Fig4B.avi